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Eco-evolutionary dynamics of plant–herbivore communities: incorporating plant phenotypic plasticity

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The interplay between evolution and ecological communities is critical for the integration of different levels of biological organization. Recent work has begun to unveil the importance of plant phenotypic plasticity and plant–herbivore (co)evolution to link plant evolution and associated insect communities. Specifically, herbivore-induced plant traits (i.e., plastic phenotypes) have significant effects on the structure and diversity of herbivore communities, which can in turn promote the evolution of not only the focal plant but also insect community members. Here, I will provide a conceptual framework on the eco-evolutionary dynamics of plant–herbivore communities to understand how biological organizations are integrated in plant–insect interactions. Research on eco-evolutionary dynamics of plant–herbivore communities will undoubtedly enrich understanding of a wide range of plant–insect interactions.

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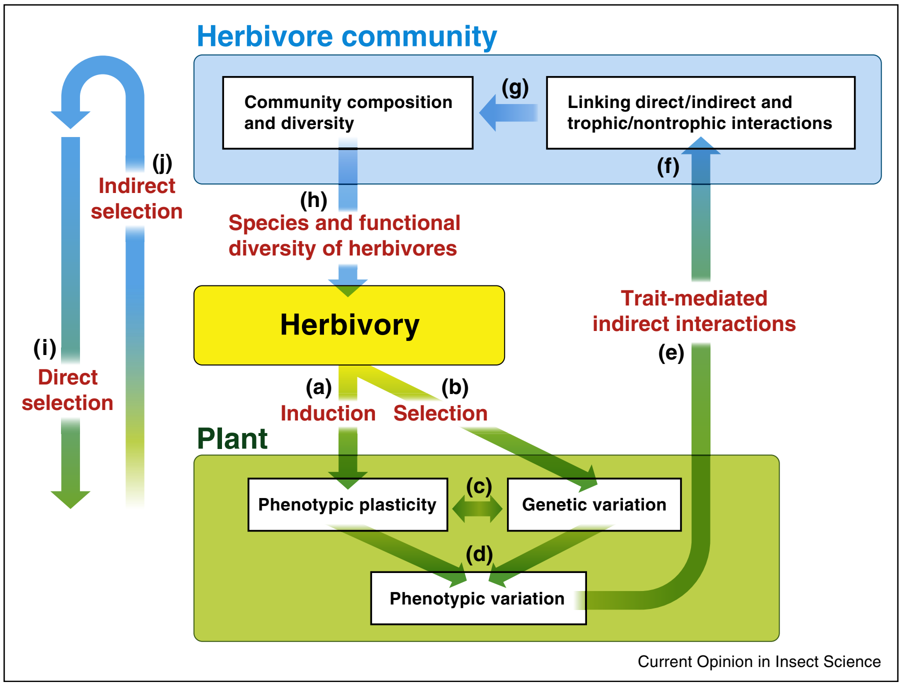
Introduction

Since there are multiple scales of biological organization from genes to ecosystems, ecologists have long recognized the importance of integrating across scales. Eco-evolutionary dynamics, the interplay of evolution and ecological processes, is critical for understanding the evolution of biological diversity, community structure, and ecosystem functions [1,2]. In this context, recent studies on plant–insect interactions have highlighted that genetic diversity in plant populations can be a driver of associated insect communities [3,4], based on the idea that plant genotypes produce phenotypic variation affecting the preference and performance of multiple coexisting insect herbivores. However, the phenotypic variation in plants is also generated by ubiquitous changes in phenotypes induced by herbivory (i.e., phenotypic plasticity) [5]. Although it is increasing evidence that plant genetic variation can shape insect communities, how this interacts with phenotypic plasticity is poorly understood [6,7•,8,9]. Although it is widely accepted that how the phenotypic and genetic variation among individuals influences population and community dynamics is critical for understanding the interplay of ecology and evolution [10–12], current eco-evolutionary dynamics research generally lacks explicit consideration of phenotypic plasticity as a source of ample phenotypic variation. To date, there are no studies documenting the consequences of phenotypic plasticity in the eco-evolutionary dynamics, except for one in a predator–prey system [13••]. Phenotypic plasticity is the property of a genotype that produces different phenotypes in response to different environments, and phenotypic variation plays an important role in creating the conditions to facilitate the process of adaptive evolution [14]. Here, I highlight the importance of herbivore-induced plant phenotypes for understanding the eco-evolutionary dynamics of plant–herbivore communities. A body of theoretical and empirical work on herbivore-induced plant phenotypes has mainly explored plant anti-herbivore defenses, with secondary metabolites involved in resistance [5] and regrowth as a mechanism of tolerance [15]. Also, there is an increasing appreciation of indirect defense; plants induce volatiles or other means (e.g., extrafloral nectaries or food bodies) when attacked by herbivores to attract natural enemies of insect herbivores [16]. Thus, I will primarily focus on the eco-evolutionary dynamics in plant–herbivore interactions based on our current understanding of inducible plant defensive traits.

Conceptual framework of eco-evolutionary dynamics of plant–herbivore communities

Plant phenotypes have significant bottom-up impacts on associated arthropod communities [17,18]. Thus, plant–insect interactions offer an ideal system to test whether induced plant phenotypes link plant evolution and insect communities. Here, I outline a conceptual framework of eco-evolutionary dynamics (feedbacks) in plant-based insect communities (Figure 1). There are two sources of the phenotypic variation in plants: genetic variation and phenotypic plasticity, both of which can be influenced by herbivory. Herbivory imposes selection on defensive genotypes and it also induces plastic trait changes. For example, rabbit grazing exerts selection on herbivore-induced tolerance traits, such as compensatory regrowth and photosynthetic rates in red fescue [19•]. As induced

Figure 1



Conceptual framework of eco-evolutionary dynamics of plant-herbivore communities. Herbivory causes phenotypic plasticity through induction **(a)** and genetic variation through selection **(b)**. As induced phenotypic plasticity has a genetic base, trait evolution may affect the likelihood and intensity of its phenotypic plasticity, whereas adaptive phenotypic plasticity in turn affects genetic variation via changing the mode of adaptive evolution **(c)**. Both are important sources of phenotypic variation in plants **(d)**. Increased phenotypic variation enhances trait-mediated indirect interactions among herbivore community members by affecting their preference and performance **(e)**, thereby linking direct/indirect and trophic/nontrophic interactions in the herbivore community **(f)**, and altering community composition and diversity of herbivores **(g)**. As for a feedback, community composition and diversity of herbivores can increase or decrease herbivory. Herbivore species identity and functional diversity influence the intensity of herbivory differently, with enhancement by synergism or reduction by antagonism among herbivores **(h)**. There are two pathways — direct and indirect — of selection of insect communities on plant trait evolution. Direct selection will occur when herbivore community properties, such as species or functional diversity, exert selection on plant traits **(i)**. By contrast, indirect selection will occur when herbivore communities induce plant phenotypes, these induced phenotypes feed back to directly exert selection on herbivore traits, and these changes in turn lead to further selection on plant traits **(j)**.

plant phenotypes have a genetic basis [20–22], trait evolution may affect the likelihood and intensity of phenotypic plasticity as a trait. On the other hand, phenotypic plasticity in turn affects the mode of adaptive evolution [14,23,24]. Increased phenotypic variation through phenotypic plasticity enhances trait-mediated indirect interactions among herbivore community members [25,26] by affecting their preference and performance, and thus links direct/indirect and trophic/nontrophic interactions [25–28]. This can alter community composition and species diversity of herbivores [29].

As for a feedback, composition and diversity of herbivore communities can increase or decrease herbivory, depending on species identity and synergism/antagonism of inducers. This is because species and functional diversity of inducers increase or decrease abundances of subsequent herbivores via herbivore-induced plant changes, resulting in different intensity of overall herbivory [25,27]. Species characteristics (e.g., foundation, keystone, and dominant species) and function (e.g., feeding modes and specialization) of inducers can influence the intensity of herbivory differently. These changes in herbivore community determine not only the strength of selection on plant traits, but also the expression of induced phenotypes. Note that there are two pathways — direct and indirect — of selection by insect communities on plant traits. Direct selection will occur when herbivore community properties, such as species or functional diversity, exert selection on plant traits. By contrast, indirect selection will occur when herbivore communities induce plant phenotypes, these induced phenotypes feed back to directly exert selection on herbivore traits, and these changes in turn lead to further selection on plant traits.

From herbivore-induced plant phenotypes to insect communities

Plant induced responses to herbivory, which increase phenotypic variation, offer a mechanistic basis for trait-mediated indirect interactions among associated